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## THE LIMITS OF ORGANIC SELECTION.

BY HENRY FAIRFIELD OSBORN,

OPENING A DISCUSSION BEFORE THE SECTIONS OF GEOLOGY AND BOTANY  
AT DETROIT.

The object of this paper is to set forth certain views as to the limits of the supplementary natural selection hypothesis recently proposed by Prof. James Mark Baldwin, Prof. C. Lloyd Morgan and myself as "Organic Selection."

The line of thought which led me to Organic Selection was as follows: The distinction between the *ontogenic* and *phylogenic variation* was drawn in my mind in 1894,<sup>1</sup> because it was evident in the current researches upon variation by Weldon, Bateson and others, and in the line of reasoning followed by Cope, Ryder, Scott, Osborn and other Neo-Lamarckians that the importance of such a distinction was being overlooked. There are three main types of variation: First, *fortuitous congenital* variations which are the temporary and transitory fluctuations around a mean. Second, *ontogenic variations*<sup>2</sup> which are the departures from normal or typical development arising during *ontogeny*; they include all the effects of the reaction of the individual to new or disturbed conditions of life which rise in the course of individual growth and may disappear with the death of the individual; the mooted question whether ontogenic variations are or are not heritable does not affect their distinctness. Third, *phylogenic variations*, also congenital, which belong in the phylum, as observed principally in fossil series; they are stable and inheritable departures from ancestral types towards a new type; they correspond with the "mutations" of Wagner and Scott, i. e., they are departures

<sup>1</sup> Alte und Neue Probleme der Phylogenese. Ergeb. d. Anat. u. Entwickl., Merkel u. Bonnet, III Band, 1893, pp. 584-625.

<sup>2</sup> Prof. C. Lloyd Morgan has proposed to apply the word "*modification*," variously used by Cope, Bailey and other authors, to what is above described as "*ontogenic variation*" and to restrict the term "*variation*" to congenital variation. This excellent suggestion subserves clearness, and should be adopted by all writers.

from ancestral types which have become permanently established. They constitute the main *evidence* for determinate variation and as a consequence determinate evolution.

In every analysis of variation these distinctions are of profound importance, because every adult organ we study (whether with Weldon it is the frontal measurement of a crab or, with Cope and Tornier, the articular facet of a bone), may be an exponent either of constitutional, phylogenic, or stirp factors, or of new environmental and ontogenic factors, or of the fortuitous or chance elements in development, or finally of all three factors combined.

In March, 1896, the application of this distinction to the problem of the *causes* of "determinate variation" was pointed out by myself in course of a discussion in the New York Academy of Sciences (p. 141) as follows: "For example, if the human infant were brought up in the branches of a tree as an arboreal type instead of as a terrestrial, bi-pedal type, there is little doubt that some of the well known early adaptations to arboreal habit (such as the turning in of the soles of the feet, and the grasping of the hands) might be retained and cultivated; thus a profoundly different type of man would be produced. Similar changes in the action of environment are constantly in progress in nature, since there is no doubt that the changes of environment and the habits which it so brings about far outstrip all changes in constitution. During the enormously long period of time in which habits induce ontogenic variations, it is possible for natural selection to work very slowly and gradually upon predispositions to useful correlated variations, and thus what are primarily *ontogenic variations* become slowly apparent as *phylogenic variations* or congenital characters of the race. Man, for instance, has been upon the earth perhaps seventy thousand years; natural selection has been slowly operating upon certain of these predispositions, but has not yet eliminated those traces of the human arboreal habits, nor completely adapted the human frame to the upright position. This is as much an expression of habit and ontogenic variation as it is a constitutional character. This fact, which has not been sufficiently emphasized before, offers an explana-

tion of the evidence advanced by Cope and other writers that change in the forms of the skeletons of the vertebrates first appears in ontogeny and subsequently at birth in phylogeny."<sup>3</sup>

On April 13, 1896, I formulated the matter in a paper before the Academy entitled "A Mode of Evolution Requiring neither Natural Selection nor the Inheritance of Acquired Characters," which has since appeared in *Science*. Professor Baldwin, of Princeton, and Professor Lloyd Morgan, of University College, Bristol, had at the same time, independently reached the same hypothesis, and Professor Baldwin has aptly termed it "Organic Selection." Both writers have presented valuable critical papers upon it, including in *Science* and *Nature* a complete terminology for the various processes involved. I concur entirely in their proposal to restrict the term *variation* to congenital variation, to substitute the term "*modification*" for ontogenic variation, and to adopt the term "*Organic Selection*" for the process by which individual adaptation leads and guides evolution, and the term "*orthoplasy*" for the definite and determinate results.

The hypothesis, as it appears to myself is, briefly, that *ontogenic adaptation is of a very profound character, it enables animals and plants to survive very critical changes in their environment. Thus all the individuals of a race are similarly modified over such long periods of time that, very gradually, congenital variations which happen to coincide with the ontogenic adaptive modifications are collected and become phylogenetic. Thus there would result an apparent but not real transmission of acquired characters.*

It is a subsidiary question whether this hypothesis is new, and a more important one whether it is true and constitutes a distinct advance towards the discovery of the unknown factors of evolution, or a satisfactory substitute for the Lamarckian theory of transmission of acquired characters.

<sup>3</sup> A writer in the *Fortnightly Review* has given a somewhat extreme illustration of the difference between ontogenic and phylogenetic progress when he says: "Man is still, mentally, morally and physically, what he was during the later Palæolithic period." "The Artificial Factor in Man." *Fortnightly Review*, October, 1896.

It appears that the idea involved in Organic Selection is by no means a new one, it is formulated, for example, but not with especial stress or clearness by Weismann in his *Romanes Lecture* of 1894, as shown in the following selections from pages 11-17 (italics our own):<sup>4</sup>

"Hermann Meyer seems to have been the first to call attention to the adaptiveness as regards minute structure in animal tissues, which is most strikingly exhibited in the architecture of the spongy substance of the long bones in the higher vertebrates. . . . But the direction, position and strength of these bony plates are by no means innate or determined in advance: they depend on circumstances. . . . It is not the particular adaptive structure themselves that are transmitted, but only the quality of the material from which intra-selection forms these structures anew in every individual life. Peculiarities of biophors and cells are transmitted, and these may become more and more favorable and adaptive in the course of generations if they are subject to natural selection. . . . *Intra-selection effects the special adaptation of the tissues to special conditions of development in each individual.* . . . Let us take the well-known instance of the gradual increase in development of the deer's antlers, in consequence of which the head, in the course of generations, has become more and more heavily loaded. . . . It is by no means necessary that all the parts concerned—skull, muscles and ligaments of the neck, cervical vertebræ, bones of the fore-limbs, etc.—should simultaneously adapt themselves by *variation of the germ* to the increase in the size of the antlers; *for in each separate individual the necessary adaptation will be temporarily accomplished by intra-selection—by the struggle of parts—under the trophic influence of functional stimulus.* . . . But as the primary variations in the phyletic metamorphosis occurred little by little, the secondary adaptations would probably, as a rule, be able to keep pace with them. *Time would thus be gained till, in the course of generations, by constant selection of those germs the primary constituents of which are best suited to*

<sup>4</sup>The Effect of External Influences upon Development. The Romanes Lecture, 1894. London, 1894.

one another, the greatest possible degree of harmony may be reached, and consequently a definite metamorphosis of the species involving all the parts of the individual may occur.

. . . . .”

What appears to be new therefore in Organic Selection is, first, the *emphasis* laid upon the almost unlimited powers of individual adaptation; second, the extension of such adaptation without any effect upon heredity for long periods of time; third, that *heredity slowly adapts itself to the needs of a race in a new environment along lines anticipated by individual adaptation, and therefore along definite and determinate lines*. This hypothesis, if it has no limitations, brings about a very unexpected harmony between the Lamarckian and ultra-Darwinian (Weismannian) aspects of evolution by mutual concessions. While it abandons the transmission of acquired characters, it places individual adaptation first and fortuitous variation second as Lamarckians have always contended, instead of placing survival conditioned by fortuitous variations first and foremost as Selectionists have contended. If true, it is thus a compromise between the pure Lamarckian and pure Darwinian standpoints in which the concessions are about equal. And if true it gives us at least a partial explanation of determinate variation which Lamarckians have recently contended for, and Darwinians have strenuously denied.<sup>5</sup>

Professor Alfred Wallace has recently endorsed this hypothesis in a review of Professor Morgan's work, "Habit and Instinct," in the March, 1897, number of *Natural Science* in the following language: "Modification of the individual by the environment, whether in the direction of structure or of habits, is universal and of considerable amount, and it is almost always, under the conditions, a beneficial modification. But every kind of beneficial modification is also being constantly effected through variation and natural selection, so that the beautifully perfect adaptations we see in nature are the result of a double process, being partly congenital, partly acquired.

<sup>5</sup> See Osborn: Cartwright Lectures, Present Problems in Evolution and Heredity, 1891. Also, "Is Variation Definite or Indefinite?" *American Naturalist*, 1889.

Acquired modifications thus helps on congenital change by giving time for the necessary variations in many directions to be selected, and we have here another answer to the supposed difficulty as to the necessity of many coincident variations in order to bring about any effective advance of the organism. In one year favorable variations of one kind are selected and individual modifications in other directions enable them to be utilized; in Professor Lloyd Morgan's words: 'Modification *as such* is not inherited, but is the condition under which congenital variations are favored and given time to get a hold on the organism, and are thus enabled by degrees to reach the fully adaptive level.' The same result will be produced by Professor Weissman's recent suggestion of 'germinal selection,' so that *it now appears as if all the theoretical objections to the 'adequacy of natural selection' have been theoretically answered.*" (Italics our own.)

Alfred Wallace thus accepts this new phase of the natural selection theory and maintains that it removes the last of the theoretical objections to the adequacy of that theory. I do not wish to be understood as taking such a sanguine view; I rather maintain the conservative position which I have held for many years in regard to the adequacy of both the Lamarckian and Darwinian theories.

Moreover, in course of discussion of this subject with my friends Professors Lloyd Morgan, Baldwin and Poulton, a very fundamental difference of opinion becomes apparent; for they agree in believing that the power of plastic modification to new circumstances, or what the Rev. Dr. Henslow has termed "self-adaptation," is in itself a result of natural selection. In other words they hold that natural selection has established in organisms this power of invariable response to new conditions, which, in the vast majority of cases is essentially adaptive. I disagree with this assumption *in toto*, maintaining that this plastic modification is, *so far as we know* an inherent power or function of protoplasm. This view, I understand, is also held by Driesch, E. B. Wilson, T. H. Morgan and probably by many others. The only cases in which self-adaptation may be demonstrated as produced by natural se-

lection are where organisms are restored to an environment which some of their ancestors experienced. We can then imagine that the adaptive response to the old environment is something which has never been lost as in the well known reappearance of the pigment in flounders.

It may be urged against the Morgan, Baldwin, Poulton views that the remarkable powers of self-adaptation, which, in many cases are favorable to the survival of the individual, are in many cases decidedly detrimental to the race, as where a maimed or mutilated embryo by regeneration reaches an adult or reproductive stage. It is obvious that reproduction from imperfect individuals would be decidedly detrimental, yet from the view taken by the above authors such reproduction would be necessary to secure the power of plastic modification for the race.

It is certain, that at the present time, one of the surest and most attractive fields of inductive research, leading towards the discovery of the additional factors of evolution or what I have elsewhere called "the unknown factor," is in experimental embryology and experimental zoology. If we could formulate the laws of self-adaptation or plastic modification we would be decidedly nearer the truth. It appears that Organic Selection is a real process, but it has not yet been demonstrated that the powers of self-adaptation which become hereditary are only accumulated by selection. They may possibly be accumulated by the inheritance of acquired modifications as Lamarck supposed.

Furthermore, another difficulty which I find with the completeness of the Organic Selection hypothesis is identical with that which almost from the outset made me hesitate in regard to the completeness of the Lamarckian hypothesis, namely, many structures, such as the teeth, which exhibit no power of self-adaptation or plastic modification during life, which are, in fact, rendered decidedly less effective instead of more effective by use and habit—these structures, I repeat, show precisely the same determinate and definite variation and consequent evolution as that which is exhibited in plastic and self-adaptive structures. This being the case, it is clear that "Organic Selec-



tion " leaves a very large field of determinate evolution entirely uncovered and unexplained, and there remains a *tertium quid* which requires further investigation. Determinate evolution in these non-plastic structures at present strikes me as part of the mechanical necessities of development, if I may so express it. That is, given a certain primitive form, there is only one route along which it can attain a certain end, provided the intervening stages are mechanically effective. It is some such law of mechanical necessity as this which out of the conical type of reptilian teeth has evolved first the triconodont type, the tritubercular, and finally the multitubercular, and from these main stages have arisen sub-stages which are repeated and independently acquired over and over again in different branches of the mammalian class. This is not an explanation, or a theory, it is a fact yet to be understood.

Organic Selection constitutes a distinct advance, and is, at least, a very useful working hypothesis, but it is by no means the conclusion of the whole matter, as Alfred Wallace maintains. We must persevere in our analysis of life processes as revealed in living organisms and in fossils with a perfectly open mind, perhaps for many decades, perhaps for another century, before we reach final conclusions in regard to the complex processes of evolution.

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## THE GEOLOGICAL CONGRESS IN RUSSIA.

By CHARLES PALACHE.

The Seventh International Geological Congress assembled in St. Petersburg during the first week of September, 1897. The Congress was notable among the meetings of this organization for the large number in attendance. It will certainly be memorable, to such of its members as took part in them, for the extent and interest of the excursions planned in con-